LARVAL DISPERSAL AS A MEANS OF GENETIC EXCHANGE BETWEEN GEOGRAPHICALLY SEPARATED POPULATIONS OF SHALLOW-WATER BENTHIC MARINE GASTROPODS [1]

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If the larvae of marine gastropods are capable of frequent long-distance dispersal, then they can be expected to serve, not only as a means of colonizing or re-colonizing new regions, but also as agents of gene flow between widely separated or disjunct populations. Populations that become completely isolated will tend to evolve in different directions. On the other hand, frequent genetic exchange between populations of the same species will counteract the divergent evolution between them, particularly if the immigrant veligers introduce especially advantageous genes upon which selection may act.

To support the hypothesis that larvae are important in maintaining genetic continuity between shoal-water populations of gastropods with amphi-Atlantic distributions, it is necessary first to give evidence that larvae are indeed dispersed over long distances and second to show that the frequency of larval dispersal is related to converging or diverging evolution of isolated adult populations of gastropod species.

Two kinds of evidence are useful in demonstrating long-distance dispersal: (1) the relationship between the circulation and the geographical distribution of larvae and (2) the duration of pelagic larval life and its relationship to the velocity of trans-Atlantic currents. Thus, larvae should be present along the entire length of the surface currents required to transport them between the geographically disjunct adult populations, and the length of pelagic larval life must be long enough so that currents will carry veligers the required distance within the time allotted them.

To understand the frequency of larval dispersal it is necessary to know: (1) the probability that larvae will survive and be transported by off-shore currents to far-distant populations and (2) the approximate number of larvae produced by the originating or parent population.

In this account I will attempt to show that larvae are dispersed over long distances, that the frequency of dispersal is much higher than might superficially be supposed, and finally, in a preliminary way, to show that the relative frequency of larval dispersal does indeed seem to be related to morphological similarities or differences found between spatially separated populations.

METHODS

The conclusions presented here are based on 857 plankton tows taken throughout the tropical and warm-temperate North Atlantic Ocean (Fig. 4). The samples were obtained from the research vessels ATLANTIS II and CHAIN by making oblique tows with a three-quarter-meter plankton net having a mesh of 223 or 316 microns. In most instances a net with the smaller mesh was used. The samples were taken

by paying out 200 meters of wire at approximately 20 meters per minute and then hauling the net inboard at a similar rate. The duration of a tow was 20 minutes and the ship moved at approximately 5.5 km/hr (3 knots). The maximum depth to which the net descended depended on current and weather conditions, but was usually about 100 meters.

Preliminary sorting was done at sea where living larvae were separated from the sample. Observations of live veligers proved to be quite valuable for later identification. Certain species were selected for rearing to settlement; these were maintained in one-liter polyethylene boxes and fed from phytoplankton cultures maintained at sea. In addition to tows made by me from the research vessels of the Woods Hole Oceanographic Institution, I have also had access to a number of other plankton samples loaned to me by various colleagues.

Very few previous taxonomic investigations have been made on tropical gastropod larvae (*vide* Simroth, 1895; Thorson, 1940; Dawydoff, 1940; Lebour, 1945), so that the adult affinities of each veliger form must be determined. Identifications can be made either by (1) comparing the larval shell with the protoconch of an adult and (2) rearing the larvae in the laboratory through settlement and post-larval development.

In practice, at least with tropical species, the latter method presents considerable difficulties. Though I have held some species of veliger larvae to settlement in the laboratory (*viz., Cymatium nicobaricum, Thais haemastoma,* and *Philippia krebsii*), generally it is not readily possible to maintain the post-larvae to a stage at which identification becomes possible, because the feeding requirements of most tropical gastropods are still quite unknown.

Identifications of the gastropod veligers considered here were made by careful comparison between larval shells and protoconchs of young adult specimens. I am indebted to the curators of molluscs, Drs. J. Rosewater, U. S. National Museum, R. T. Abbott and R. Robertson, Academy of Natural Sciences of Philadephia, and W. J. Clench and K. J. Boss, Museum of Comparative Zoology, Harvard University, for allowing me the use of collections under their custody. Mr. H. Lewis of the Philadelphia Shell Club kindly made specimens of Cymatiidae available to me. Usable specimens having protoconchs in good condition are relatively rare for most species. In identifying any species of larva, I have looked at the protoconch of specimens of all other closely related species that occur in the tropical and warm-temperate Atlantic if the material were available.

Results and Discussion

Evidence for long-distance larval dispersal

The relationship between circulation and geographical distribution of larvae

The importance of larval dispersal was already recognized by Alfred Russel Wallace in his work on *The Geographical Distribution of Animals* (1876). Wallace knew that the univalve and bivalve Mollusca have free-swimming larval stages and recognized that "they thus have a powerful means of dispersal, and are carried by tides and currents so as ultimately to spread over every shore and shoal that offers conditions favorable for development." (Vol. I, page 30). Simroth (1895)

described and figured pelagic Mollusca, including gastropod veliger larvae, from samples taken on the *Plankton Expedition*, though he did not establish the identity of most of the forms he described. Thorson (1961, page 466) recognized that certain genera of gastropods, principally tropical in their geographical distribution (*e.g., Lamellaria, Tonna, Cassis, Charonia, Cymatium,* and *Bursa*), have larvae that "have been found midway across the oceans." Recently, Robertson (1964) and Scheltema (1964, 1966a) have described the dispersal of two species of gastropods into the Sargasso Sea and Gulf Stream, while Mileikovsky (1966) has reviewed existing knowledge on the dispersal of molluscan larvae, particularly the dispersal of prosobranch veligers in the Norwegian Sea. The gastropod families that are now known to have representatives with long pelagic developments include the families Neritidae and Naticidae (first mentioned here), and the Triphoridae, Lamellariidae, Architectonicidae, Cymatiidae, Cassidae, Tonnidae, Muricidae, Bursidae, Coralliophilidae, Ovulidae, and Cypraeidae (Scheltema, 1966b).

While scattered records have already shown the existence of larvae in the open sea, no systematic attempt has yet been made to determine their occurrence over large areas of the ocean and in particular their presence throughout the entire length of major current systems of the equatorial and north temperate Atlantic Ocean. These data are the most important in demonstrating the dispersal of larvae over long distances.

The evidence from plankton collections I have made shows that dispersal of gastropod larvae into the open sea is not a rare event but a commonplace occurrence (Fig. 4). Taking into account all collections examined, including samples from all major currents of warm waters of the North Atlantic Ocean, 70 per cent contain gastropod larvae from the shoal-water benthos. Many species are found during all months of the year. Because of their common occurrence and in order to avoid the cumbersome expression "long-distance larvae from shoal-water bottom-dwelling organisms of the shelf," I have applied to these open-sea forms the term *teleplanic larvae* or *teleplanos* (from the Greek *telep'lanos,* meaning far-wandering) (Scheltema, in press). The teleplanos may be defined as larvae that (1) originate from shoal-water, continental-shelf benthos, (2) are regularly found in the open sea, (3) have a pelagic development of long duration, and (4) serve as a means for dispersal over long distances. The term is not restricted taxonomically to any phylum, but specifically excludes larvae of the holoplankton. Many teleplanic gastropod veligers have morphological adaptations which enhance their survival on the open ocean, such as long periostracal spines, the reduction or complete lack of shell calcification, and an increase in length of the velar lobes used for swimming and feeding.

The North Atlantic circulation. The direction and route of larval dispersal are determined by the principal ocean currents. The circulation of the North Atlantic Ocean may be regarded as an enormous anticyclonic gyre. On the west is the Gulf Stream moving northeastwardly; on the north is the North Atlantic Drift moving toward the east and dividing into a northern and southern arm; bounding the eastern portion of the gyre is the Canary Current moving to the southwest; and finally on the south is the North Equatorial Current moving westwardly across the tropical North Atlantic toward the West Indies (Fig. 4). Details of this circulation are obviously much more complex. Large temporary eddies

are known to occur in the Gulf Stream (Fuglister, 1963) and the North Atlantic Drift is grossly over-simplified by this description (*vide* Worthington, 1962; Mann, 1967). Notwithstanding, this generalized conception allows prediction of the transport expected from an object floating on or near the ocean surface. In the Equatorial Atlantic Ocean the North Equatorial Current is separated from the westwardly flowing South Equatorial Current by a weakly developed Equatorial Countercurrent flowing toward West Africa. The Countercurrent moves only a relatively small volume of water and is seasonal in occurrence (Schumacher, 1940, 1943; *U. S. Hydrographic Office Monthly Pilot Charts*). However, directly beneath the westwardly flowing South Equatorial Current a strong eastwardly moving Equatorial Undercurrent flows from South America toward the island of São Tomé off West Africa (Voorhis, 1961; Voigt, 1961; Metcalf, Voorhis and Stalcup, 1962; Khanaychenko, Khlystov and Zhidov, 1965; Rinkel, Sund and Neuman, 1966; Strum and Voigt, 1966). This warm, shallow current (20° to 27° C), whose core extends between 50 and 100 meters depth, provides a means whereby tropical larvae may be dispersed from west to east across the tropical Atlantic (Chesher, 1966, page 210; Scheltema, 1968).

Description of larvae and their geographical distribution in the North and Equatorial Atlantic Ocean. To illustrate specific instances of teleplanic gastropod larvae in temperate and tropical Atlantic waters, I have selected to consider in detail, from among many species, ten representative forms taken from the families Cymatiidae, Tonnidae, Cassidae, Muricidae, Architectonicidae, and Neritidae. Since the larvae of these ten species are either completely unknown or not previously well described, each is illustrated and briefly described here.

Family Cymatiidae

The family Cymatiidae or hairy tritons is a group of carnivorous gastropods which are very well represented in the tropical Atlantic. The three species considered here, *Cymatium parthenopeum* (von Salis), *Cymatium nicobaricum* (Röding), and *Charonia variegata* (Lamarck), all have very wide geographical distributions. *Cymatium parthenopeum* is known throughout most of the warm and tropical North and South Atlantic and as *Monoplex australasiae* Perry in the Indo-Pacific (Clench and Turner, 1957). *Cymatium nicobaricum* is common in the western Atlantic and Indo-Pacific but has also been reported from a few records in the eastern Atlantic (Dautzenberg, 1890; Odhner, 1931; Clench and turner, 1957). The egg masses of several Cymatiidae are known from recent studies of Laxton (1969).

The larva of *Cymatium parthenopeum* has an uncalcified, resilient, translucent, amber-colored, conical, multispiral shell which becomes somewhat darker in color when nearing completion of planktonic development (Fig. 1, d, e, f). The first whorl following the embryonic shell is cancellate; the remaining whorls are glossy and smooth (Fig. 1, j). The shell in early stages is holostomatous, becoming siphonostomatous with a short siphonal canal when reaching the intermediate stage (Fig. 1, d; see also Scheltema, 1966a, Figs. 4a and 4b). The outer lip has a varix when larval growth is completed (Fig. 1, e, f). The slightly impressed suture of the body whorl is mostly obscured by the smooth, overlying
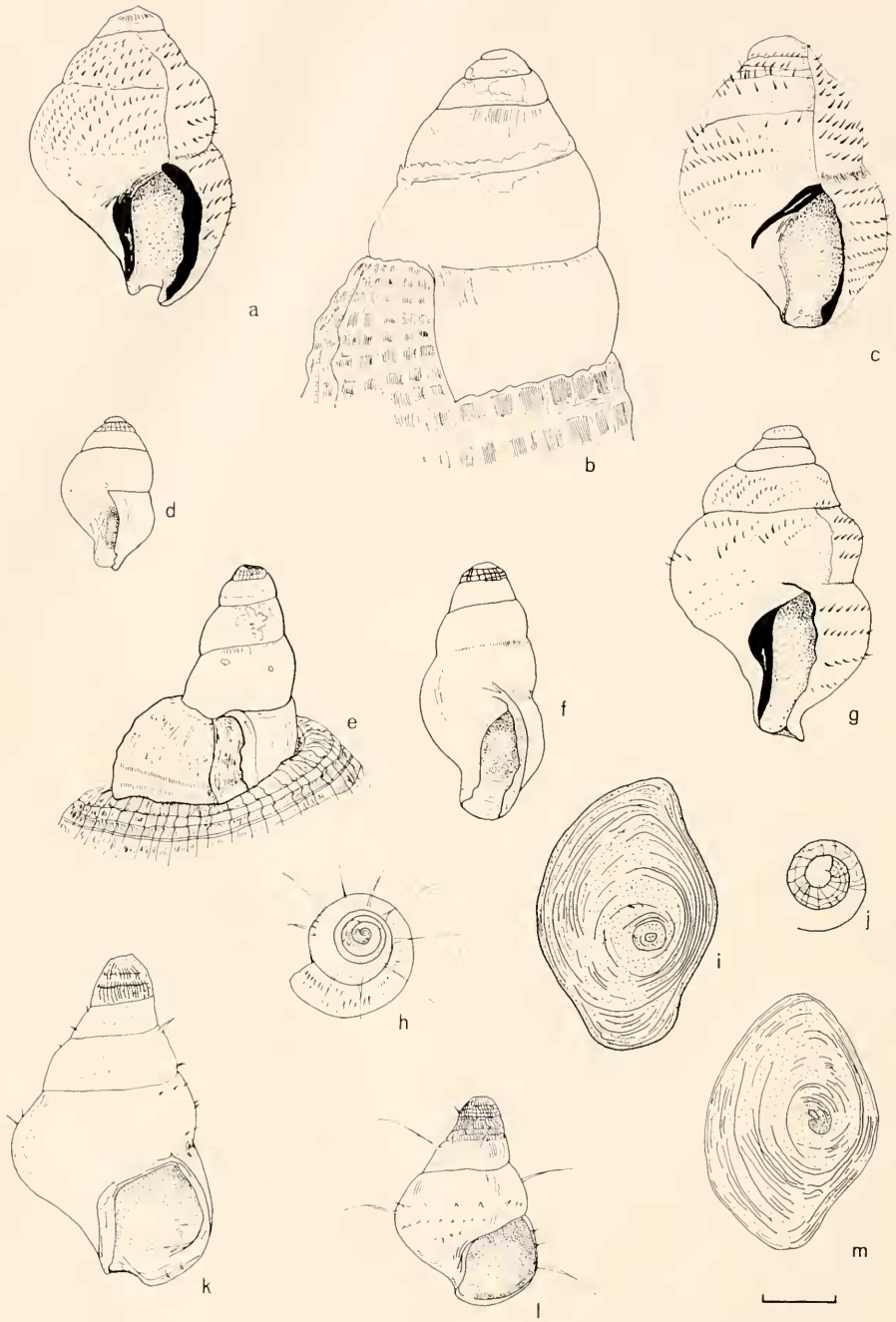
Figure 1.

periostracum. The operculum shows practically no markings; a very faint eccen-
tric nucleus is sometimes visible. In the living larva the body is light cream-
colored, while the foot is gray to black. The larva has two tentacles and four
long velar lobes lacking pigmentation (*vide* Scheltema, 1966a, Fig. 2). When
growth is completed the larval shell is about 3.5 mm in length. The unknown
larval shell figured by Simroth (1895, Table V, Fig. 16) is probably this
species. The teleplanic larvae of *Cymatium parthenopeum* are found throughout
the North Atlantic gyre, in the Caribbean, and from two locations in the western
end of the south Equatorial Current (Fig. 5).

The larva of *Cymatium nicobaricum* was described by Lebour (1945, pages
477–478, Fig. 24, as *Cymatium chlorostomum*) from the waters near Bermuda,
and the species was also figured but unidentified by Simroth (1895, Pl. V, Figs. 10
and 11). It is very easily recognized because it is the only *Cymatium* larva in
the Atlantic having a coeloconoid shell (Fig. 1, k, 1). The first 1½ whorls
following the embryonic shell are cancellate. On the completely developed larva
the embryonic and sometimes a portion of the cancellate whorls are already worn.
The early and intermediate stage larvae have long, slightly curved, periostracal
spines (Fig. 1, h, 1) which in older larvae may no longer be present (Fig. 1, k).
Minute axial lines are sometimes barely visible in the periostracum. The oper-
culum (Fig. 1, m) differs from most Cymatiidae in that its nucleus is only very
slightly eccentric. Only *Charonia variegata* has a similar operculum (Fig. 1, i),
but the larvae of *Cymatium nicobaricum* cannot be confused with this species.
In the living larva of *Cymatium nicobaricum* the body pigmentation is pink with
darker reddish patches. There are four long velar lobes which completely lack
pigmentation. The length of the fully grown larval shell is about 4.6 mm. It is
very often encrusted with fouling organisms including Folliculinidae, green algae,
and encrusting bryozoa. *Cymatium nicobaricum* larvae are restricted in the
samples to the western Atlantic and North Atlantic Drift (Fig. 5) but were never
found in the eastern Atlantic.

Charonia variegata has the largest known larvae of any of the Cymatiidae in
the Atlantic, the shell exceeding 5 mm in length when fully developed. Its ovate,

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FIGURE 1. Larval shells, opercula and protoconchs of three species of Cymatiidae: (a)
larval shell of *Charonia variegata*, Northwestern Atlantic, 39°27′N, 50°17′W; (b) protoconch
of *Charonia variegata*, Western Atlantic, Tobago Island, B.W.I. (ANSP 209812); (c) *Cha-
ronia variegata* larval shell, North Equatorial Current, 19°11′N, 47°24′W; (d) intermediate
stage veliger larva of *Cymatium parthenopeum*, Gulf Stream, 38°43′N, 70°46′W; (e) proto-
conch of *Cymatium parthenopeum*, collection of H. Lewis (No. 2493); (f) late veliger larva of
Cymatium parthenopeum at final stage before settling, off the Azores, 36°32′N, 30°14′W; (g)
larva of *Charonia variegata*, Eastern Atlantic off the West Coast of Africa, *Atlantide* Station
No. 122, 01°29′S, 08°50′E; (h) apical view of intermediate stage larva of *Cymatium nicobari-
cum*, Gulf Stream, 35°44′N, 66°53′W; (i) operculum from larva of *Charonia variegata*, internal
view, specimen from same station as (a) above; (j) embryonic shell and first cancellate whorl
of the pelagic larva of *Cymatium parthenopeum*, Gulf Stream, same station as (d) above; (k)
late veliger larva of *Cymatium nicobaricum* at final stage before settlement, Western Atlantic
near Bermuda, 32°45′N, 64°36′W; (1) intermediate stage larva of *Cymatium nicobaricum*,
Western Atlantic, Gulf Stream, same station as (h) above; (m) operculum from larva of
Cymatium nicobaricum, internal view, specimen from same station as (h) above. Scale = 1 mm
in all figures except i, j, and m where it is equivalent to 0.5 mm. Numbers prefixed by
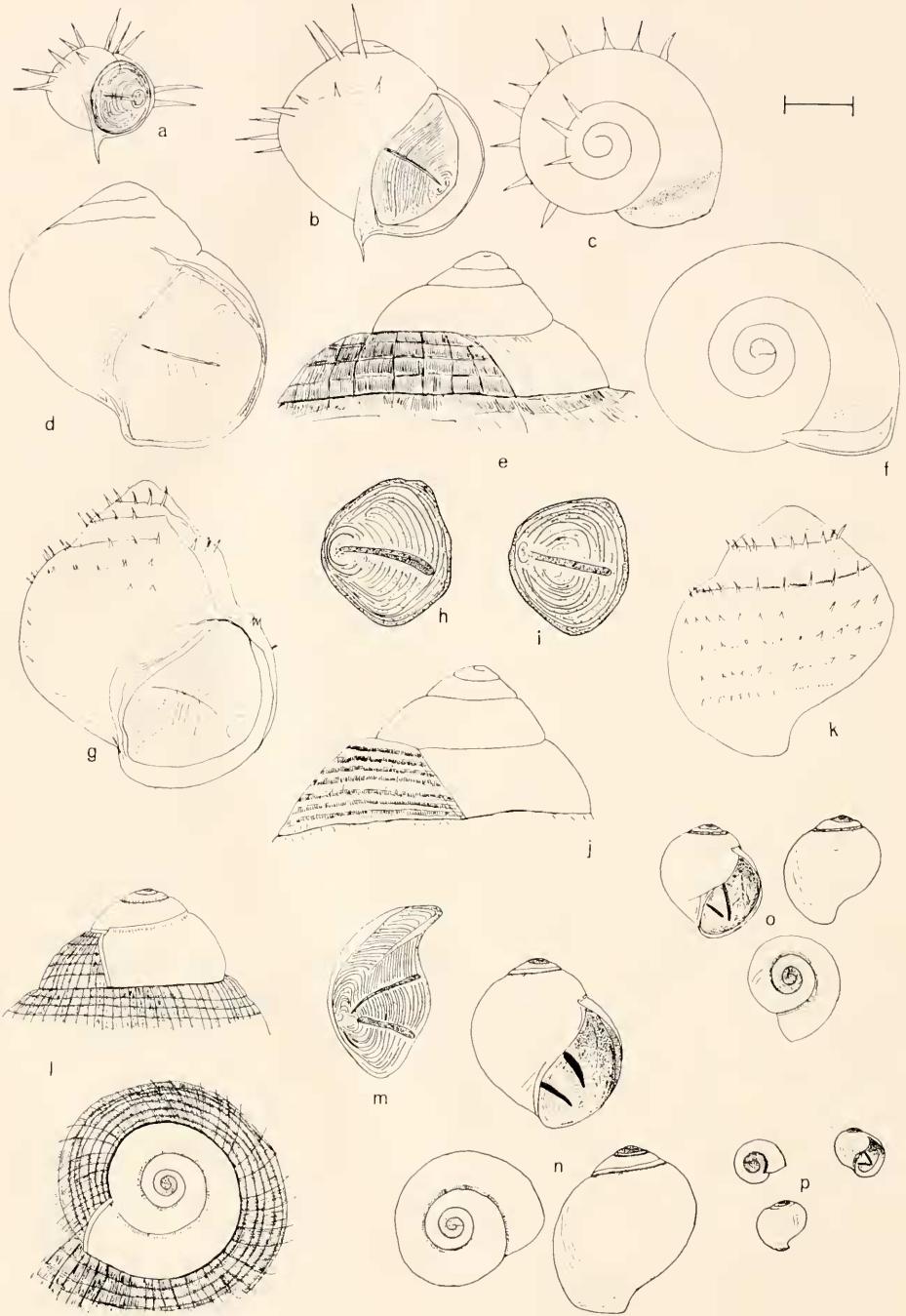"ANSP" are lot numbers in the Academy of Natural Sciences of Philadelphia.

Figure 2.

hairy shell is dark amber-brown, barely translucent, and uncalcified in the early stages. The protoconch found on museum specimens of this species is smooth and secondarily calcified from within, giving a rather massive appearance (Fig. 1, b). Sometimes there is evidence of periostracal fragments adhering to the proto-conch, remains of the elaborate pattern of short, soft spines which give the larvae a hirsute appearance (Fig. 1, a, c, g). The whorls directly following the embryonic shell are cancellate but usually already worn in late larval development (Fig. 1, a). The last three whorls are shouldered. The sutures are normally obscured by the periostracum, which is continuously laid down with the growth of each succeeding whorl. In early larvae the periostracal spines on the first two or three whorls directly following the cancellate whorl are more or less axially arranged (Fig. 1, a). In succeeding whorls the periostracal spines are spirally arranged (Fig. 1, c). With growth of the larva the periostracum of the adapical whorls is overlain with new periostracum upon which the spines are also spirally arranged. On older and larger larval shells the outer parietal lips are glossy and semitransparent in transmitted light but appear very dark brown in reflected light. The operculum of the larva is characteristic, having the nucleus almost central as it also is in the adult (Fig. 1, i; *vide* Clench and Turner, 1957 for illustration of adult operculum). This is probably the species figured but unidentified by Simroth (1895; Pl. VI, Figs. 1–5). Since the protoconch of the eastern Atlantic species *Charonia nodifera* (Lamarck) has not been seen, it is not certain that the larval shell of this species can be separated from *Charonia variegata*. Variations in shell morphology are not consistently related to the geographical distribution of the larvae, and therefore two species of veligers are not distinguishable. The dispersal of *Charonia variegata* larvae by ocean currents is very evident from their widespread geographical dis-tribution throughout the North Atlantic gyre, in the South Equatorial Current, and from scattered records in the Caribbean Sea (Fig. 6).

FIGURE 2. Larval shells, opercula and protoconchs of the Tonnidae and Cassidae: (a) larval shell of the early intermediate stage veliger of *Tonna galea,* Sargasso Sea east of Ber-muda, 32°05'N, 59°10'W; (b) intermediate stage larva of *Tonna galea,* North Equatorial Cur-rent, 24°34'N, 47°20'W; (c) intermediate stage larva of *Tonna galea,* same specimen as (b) above; (d) shell of fully developed veliger larva of *Tonna galea,* Western Atlantic, Gulf Stream, 36°22'N, 67°53'W; (e) protoconch of *Tonna galea,* apical angle 105°, Western At-lantic, S. Inlet, Lake Worth, Boynton, Florida (ANSP 181564); (f) apical view of fully grown larva of *Tonna galea,* same specimen as (d) above; (g) larval shell of fully grown veliger, *Tonna maculosa,* Western Atlantic, Sargasso Sea, 25°05'N, 57°48'W; (h) larval operculum of intermediate stage veliger of *Tonna maculosa,* viewed from inside, specimen from Gulf Stream between Cape Cod and Bermuda; (i) larval operculum of intermediate stage veliger of *Tonna galea,* viewed from inside, specimen from Gulf Stream between Cape Cod and Bermuda; (j) protoconch of *Tonna maculosa,* apical angle 94°, Western Atlantic, Key West, Florida (Scheltema coll.); (k) larval shell of fully grown veliger, *Tonna maculosa,* same speci-men as (g) above; (l) two views of the protoconch of *Phalium granulatum,* Western Atlantic, Matthew Town, Great Inagua, Bahamas (ANSP 173078); (m) operculum from larva of *Phalium granulatum,* viewed from inside, specimen from North Atlantic Drift, 44°11'N, 44°11'W; (n) three views of fully developed larva of *Phalium granulatum,* off the West Afri-can coast, 20°32'N, 22°34'W; (o) three views of intermediate stage larva, *Phalium granulatum,* Western Atlantic, Gulf Stream, 38°17'69°36'W; (p) three early stage larvae of *Phalium granulatum,* Western Atlantic, northern end of Gulf Stream, 41°14'N, 57°28'W. Scale = 1 mm in all figures except m, where it is equivalent to 0.5 mm. Numbers prefixed with ANSP refer to museum lot numbers in the collection of the Academy of Natural Sciences of Phila-delphia.
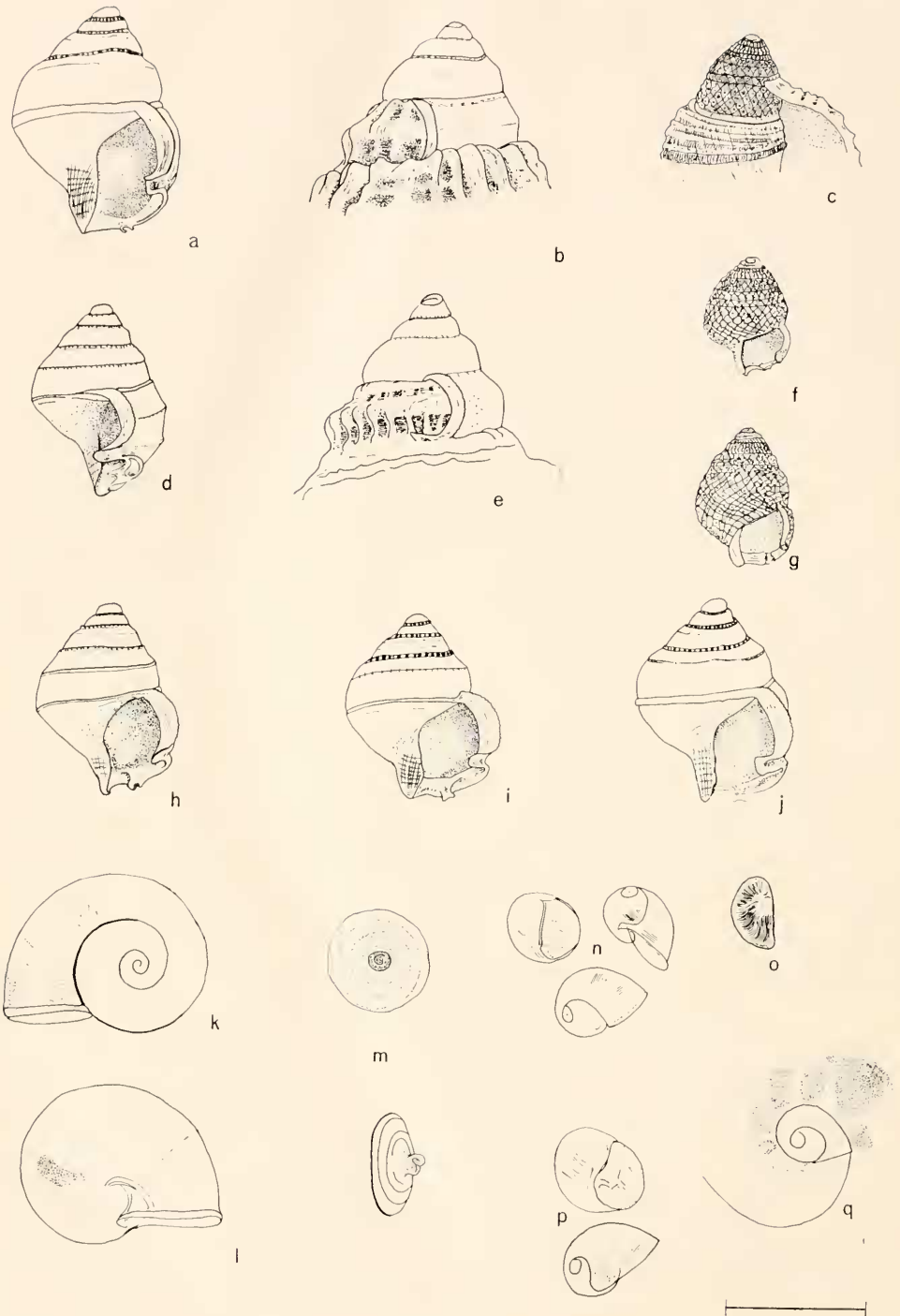
FIGURE 3.

Family Tonnidae

The Tonnidae or tun shells are large gastropods found in tropical and warm temperate waters throughout the world. Members of this family are restricted to the continental shelf and occur mostly on sandy bottoms. Little is known regarding the life history of most species. Thorson (1940, pages 192–193) has figured the egg mass and early larva of *Tonna* (?) *maculosa* while Knudsen (1950, pages 97–98, Fig. 8) shows an egg mass that he attributes to *Tonna costatum* (Menke). These flat gelatinous masses with "egg spaces" containing about 100 eggs each may have from 350–660 thousand embryos. The eggs are relatively large, 300 microns in diameter, and the early larvae of *Tonna* (?) *maculosa* illustrated by Thorson (1940, page 193, Fig. 15) is about 380 microns in longest dimension. Measurement of the embryonic shell on *Tonna galea* closely corresponds to this, being about 400 microns in length.

The two equatorial Atlantic species are *Tonna galea* (Linné) and *Tonna maculosa* (Dillwyn). Larvae of both these species are encountered in the Gulf Stream.

The early intermediate stage larva of *Tonna galea* has long, straight, fairly stout, spirally arranged, periostracal spines. This stage appears to be similar to that illustrated by Lebour (1945, page 475, Fig. 21) as *Tonna perdix* (Linné). In the later intermediate stage larva, as a new whorl is added, additional spines are also formed (Fig. 2, b, c). The globose shell is smooth, white, and glossy. When completely developed the larva has usually lost all its periostracal spines and then measures about 3.5 mm in length (Fig. 2, d, f). The typical long, drawn-out basal periostracal spine seen in the earlier stages is also frequently lost. At this late stage of development the larva of *Tonna galea* may be confused with that of *Tonna maculosa*. The two differ, however, in the shape of the aperture

FIGURE 3. Larval shells, opercula and protoconchs of some species belonging to the families Muricidae, Ovulidae, Architectonicidae, and Neritidae: (a) *Thais* (?) *rustica* veliger larva, Eastern Atlantic from off West Africa, 22°59′N, 20°30′W; (b) protoconch of *Thais rustica*, Western Atlantic, Port Royal, Jamaica (USNM 442303); (c) protoconch of *Pedicularia sicula decussata*, off coast of Georgia, Western Atlantic, depth 792 m, U. S. Fish. Comm. Sta. No. 2415 (USNM 108408); (d) *Thais haemastoma* larval shell, Western Atlantic east of Bahamas, 25°06′N, 67°42′W; (e) protoconch of *Thais haemastoma*, Western Atlantic, Corpus Christi Bay, Texas (USNM 125561); (f) larval shell of *Pedicularia sicula*, Western Atlantic, Gulf Stream, 36°27′N, 68°01′W; (g) larval shell of *Pedicularia sicula*, Eastern Atlantic, off Azores, 37°14′N, 27°44′W; (h) larval shell of *Thais haemastoma*, Western Atlantic east of Bahamas, same station as (d) above; (i) larval shell of *Thais haemastoma*, Mid-equatorial Atlantic, South Equatorial Current, 02°34′N, 24°03′W; (j) larval shell of *Thais haemastoma*, Eastern Atlantic off West Africa, 08°00′N, 15°15′W; (k) *Philippia krebsii* larval shell, fully developed, Western Atlantic, North Atlantic Drift, 39°26′N, 44°05′W; (l) *Philippia krebsii* larval shell, same as (k) above; (m) operculum of *Philippia krebsii*, inner view and side view showing apophysis; (n) three larval shells of *Smaragdia viridis*, Western Atlantic, Gulf Stream, 30°40′N, 73°40′W; (o) operculum taken from larva of *Smaragdia viridis*, northern end of Gulf Stream, Western Atlantic, 41°26′N, 55°45′W. Arrow shows position of minute reinforcing bar; (p) two larval shells of *Smaragdia viridis*, Eastern Atlantic off West Africa, 07°20′S, 07°23′E; (q) protoconch of *Smaragdia viridis viridemaris* showing larval shell slightly immersed, Western Atlantic, Castle Harbor, Bermuda, depth 7–9 m (ANSP 267608). Scale = 1 mm for all figures. Numbers prefixed by "ANSP" refer to lot numbers in the collection of the Academy of Natural Sciences of Philadelphia. Numbers prefixed by "USNM" are lot numbers from the collection of the United States National Museum, Washington, D. C.

(compare Fig. 2, d with 2, g); the length, number, and angle of the spines (if still present, Fig. 2, k); the apical angle of the spire, usually greater than 100° in *Tonna galea* (Fig. 2, d, e) and less than 100° in *Tonna maculosa* (Fig. 2, g, j); and the shape of the reinforcing bar on the operculum whereby it is attached to the foot musculature (Fig. 2, h, i), being curved in *Tonna maculosa* but straight in *Tonna galea*. Simroth (1895, Pl. IV) under the larval name *Macgillivrayia* has figured *Tonna* larvae. The large operculum (Pl. IV, Fig. 7) is that of *Tonna galea*, but Figs. 1–3 on the same plate are probably *Tonna maculosa*. Larvae of *Tonna galea* were found throughout the North Atlantic gyre, in the South Equatorial Current, off the west coast of Africa, in the mid tropical Atlantic, off the northeast coast of Brazil, and in the Caribbean Sea, whereas those of *Tonna maculosa* were found only in the western Atlantic (Fig. 7).

Family Cassidae

The family Cassidae, known in the vernacular as helmet or bonnet shells, is closely related to the two preceding families (*i.e.,* Tonnidae and Cymatiidae) and like them has a worldwide distribution in tropical and warm temperate waters. The adults live on sandy bottoms or in *Thalassia* beds and feed upon echinoids. The egg mass of *Phalium granulatum* is made up of capsules built into tower-like structures (*vide* Abbott, 1968, Pl. I), and has up to 300 eggs in each capsule. The larvae most frequently encountered in the North Atlantic that belong to the family Cassidae are those of *Phalium granulatum* (Born). This larva is smaller than any of those previously considered here, the shell being somewhat less than 2.5 mm at settlement. The shell is globose (Fig. 2, n, o), though with a somewhat flattened spire, particularly in earlier stages (Fig. 2, p). The sutures are adpressed; the first $1\frac{1}{2}$ whorls are amber-brown while the remainder of the shell is smooth, glossy, and white. The operculum (Fig.2, m) is distinctive with its two strengthening supports.

Two other species of *Phalium* occur in the tropical North Atlantic, (1) *Phalium coronadoi* (Crosse), a rarely collected species known only from the coast of North Carolina and Cuba, and (2) *Phalium saburon* (Bruguière), a species whose distribution overlaps that of *Phalium granulatum*, being found in the Azores, Bay of Biscay, and southward along the west coast of Africa to Ghana. Protoconchs of both these species have been examined and compared to *Phalium granulatum* (Fig. 2, 1); *Phalium coronadoi* and *Phalium saburon* both have smaller larvae with wider apical angles.

The geographical distribution of *Phalium granulatum* veliger larvae includes the Gulf Stream, the North Atlantic Drift, the Canary Current off the west coast of Africa, and the South Equatorial Current (Fig. 8).

Family Muricidae

The Muricidae are a family of carnivorous gastropods which feed on bivalves, barnacles, and other gastropods. The genus *Thais* (sometimes relegated to a separate family Thaididae) is represented in the tropical Atlantic by at least four very common species which definitely are known to have pelagic phytoplanktotrophic larvae. The egg capsules of the various species of *Thais* are laid singly

rather than in distinctive masses as in some of the Cymatiidae and in *Phalium granulatum* and in most species are usually between 5 and 8 mm in height.

The larval shell of *Thais haemastoma* (Linné) was illustrated by Craven in 1877 as the species *Sinusigera colbeauiana*. Later in 1883 he figured an early post-larval shell which this time he correctly identified as *Thais haemastoma*. Dautzenberg (1889, Pl. II, Fig. 5) has figured an early post-larval shell from the Azores showing details of the protoconch of *Thais haemastoma*. Recently Moore (1961) accurately described the shell of the fully developed larva, but his

FIGURE 4. Geographical distribution of plankton tows upon which the present study is based. The darkened circles indicate stations where teleplanic gastropod veligers were found; the open circles denote stations where no such gastropod larvae were taken. In instances when plankton tows were less than one degree apart, points shown on the above and subsequent charts may represent more than one tow. Some stations were repeated at the same location at different times of the year. Locations included in the figure are only those for which entire plankton samples have been examined. Stations appearing on subsequent charts but not on this figure represent positive records from loaned plankton tows. They were not used for negative records because material had been previously sorted from them or preservation was poor, and because they had been collected differently. The dashed lines indicate the 21° C summer and winter isotherms. Major surface currents in the North and tropical Atlantic are designated by arrows and may be identified by reference to letters: A = Gulf Stream, B = North Atlantic Drift, C = Canary Current, D = North Equatorial Current, E = Equatorial Countercurrent, and F = South Equatorial Current.

accompanying illustration (page 26) is confusing and lacks necessary details of shell ornamentation.

The larval shell of *Thais haemastoma* at the completion of growth is about 1.5 mm in length (Fig. 3, d, h, i, j). There are five whorls and an apical embryonic shell. The base of the columella has a cancellate pattern formed from seven or more axial and about an equal number of spiral cords. Below the sutures there are minute axial riblets. The third whorl has a single ribbed spiral cord which continues on the succeeding whorls. The larva is a typical *Sinusigera* with a long projection separating the adapical from the basal portion of the outer lip. A varix, frequently with a serrate adapertural edge, is formed in the adapical portion of the outer lip. The body whorl may have minute punctae extending back about ¼ whorl from the edge of the outer lip. The body whorl is bounded adapically by a spiral band which is continuous with the varix. Certain minute features are lost with preservation and the shell tends to become "chalky" with time.

There are closely related species in the *Thais haemastoma* complex (*e.g.*, *Thais rustica* [Lamarck], *vide* Clench, 1947) which seem to have larvae quite similar to *Thais haemastoma senso stricto* (compare Fig. 3, b and 3, e; the latter protoconch is worn). Certain larvae which were taken off the west coast of Africa and which otherwise appeared identical, differed in having a less calcified shell, being slightly larger, having a somewhat greater apical angle, and having a narrower varix lacking a serrate edge (Fig. 3, a, off west Africa should be compared with Fig. 3, d, h, i, j). These somewhat different west African larvae most closely resemble the protoconch of *Thais rustica*, though this species in the eastern Atlantic has been reported only from St. Helena.

The geographical distribution of *Thais haemastoma* larvae includes the Gulf Stream, the North Altantic Drift, the Canary Current, and the South Equatorial Current (Fig. 9).

Family Architectonicidae

Architectonicidae or sundial shells are a family of subtidal gastropods represented in tropical waters throughout the world. Some subtropical and warm temperate forms are also found. The adults of most known species are restricted to depths of a few meters to about 200 meters near the edge of the continental shelf. Their food is apparently confined to coelenterates, particularly the zoanthid genera *Palythoa* and *Zoanthus* (Robertson, 1967) and also the polyps of scleractinians and actiniarians (Robertson, Scheltema and Adams, 1970). Many Atlantic species are now known to have teleplanic larvae. Moreover, of the ten species found by Marche-Marchad (1969) along the coast of west Africa, seven are also known from the West Indies. The larvae of at least some of these species are eurythermal. *Philippia krebsii* has been found in temperatures from 18.9 to 28.9° C. Other architectonicid larvae have been found at temperatures as low as 13.5° C.

The larval shell of *Philippia krebsii* (Mörch) is illustrated by Robertson (1964, Fig. 4 and Figs. 7–10) and Robertson *et al.* (1970, Figs. 3 and 6). It is hyperstrophic, smooth, glossy, and more or less transparent (Fig. 3, k, 1). The operculum is circular, externally concave, with a central internal apophysis that extends into the foot musculature (Fig. 3, m). The apophysis is constricted

at the base as is also found in the adults belonging to the subgenus *Psilaxis* (Robertson, 1970a, Fig. 10, page 74). The living larva has four velar lobes with pale orange pigmentation along their borders. The anterior of the foot is darkly pigmented except for a conspicuous white food-rejection tract passing from beneath

FIGURE 5. Geographical distribution of the larvae of *Cymatium parthenopeum* (von Salis) and *Cymatium nicobaricum* (Röding): 1 = stations with *Cymatium parthenopeum*, 2 = stations with *Cymatium nicobaricum*, 3 = stations where both species were taken. Small open circles are stations where neither species was encountered in tows. Stippled areas show the approximate geographical regions where adult *Cymatium parthenopeum* is to be found to depths of 63 meters (Clench and Turner, 1957). The geographical distribution of post-larval *Cymatium nicobaricum* roughly corresponds to that of *Cymatium parthenopeum* in the western Atlantic, but in the eastern Atlantic *Cymatium nicobaricum* is known only from the Madeira and Canary Islands (Clench and Turner, 1957; Odhner, 1931; Dautzenberg, 1890). Arrows show direction of surface currents.

the mouth to the anterior base of the foot. *Philippia krebsii* is readily distinguished from other species of Architectonicidae in the Atlantic by its large size (1.5 mm along the longest axis) and by the presence of a prominent anal keel (*vide* Robertson, 1964, page 6, Table I). The geographical distribution of *Philippia krebsii* larvae essentially includes all the major surface currents of the tropical and temperate North Atlantic Ocean (Fig. 10).

Family Neritidae

The larval shell of the neritid *Smaragdia viridis* is smooth, glossy white with adpressed sutures (Fig. 3, n, p, q). The embryonic shell is only 120 microns longest dimension, but the fully developed larva is 650 microns along this axis. The living larva has a simple bilobed velum and two small tentacles. The digestive gland has a green, almost chartreuse, cast which is retained for several months after preservation. The small operculum is paucispiral and has a minute reinforcing bar next to the nucleus (Fig. 3, o, see arrow). In later life the adult shell is cryptically colored and is frequently found associated with *Thalassia* in the western Atlantic and *Posidonia* in the Mediterranean. Possibly it may be dispersed on drifting turtle grass (*vide* Menzies, Zaneveld and Pratt, 1967).

The geographical distribution of *Smaragdia viridis* veliger larvae includes the Gulf Stream, the western portion of the North Atlantic Drift, the Canary Current, the South Equatorial Current, and Caribbean Sea (Fig. 11).

Family Ovulidae

The veliger larva of the ovulid *Pedicularia sicula* Swainson is an ovate, amber-brown *Sinusigera*. The embryonic shell, somewhat lighter in color and approximately 125 microns in length, is followed by two spiral whorls with axial costae and a single spiral cord. The two remaining whorls have oblique reticulate ornamentation (Fig. 3, f, g). Sometimes this ornamentation becomes interrupted and confused. The outer lip of the fully developed larval shell has a thickened varix and the typical beak, a projection found on all *Sinusigera*-type veligers. The fully developed larval shell is between 0.9 and 1.0 mm in length.

The protoconch of the post-larva, as is common to members of the Cypraeidae and Ovulidae, becomes completely hidden in the adult by succeeding whorls. It is therefore necessary to have relatively young specimens for comparison with the larva (Fig. 3, c).

A number of names have been applied to the species *Pedicularia sicula* (*vide* Allen, 1956). The limited amount of material examined reveals no good reason for separating the eastern and western Atlantic forms of *Pedicularia* into separate species, and the western Atlantic form, usually known as *Pedicularia decussata* (Gould), should probably be considered no more than a subspecies of the eastern Atlantic and Mediterranean *Pedicularia sicula*. Specimens of North Atlantic species are rare in museum collections so the degree of variability is not well understood.

The protoconch of a Pacific species of *Pedicularia* was first figured by John Dennis MacDonald (1858), assistant-surgeon on H. M. S. HERALD in a paper entitled, "On the probable metamorphosis of *Pedicularia* and other forms; affording presumptive evidence that the pelagic Gastropoda, so called, are not adult forms, but, as it were, the larvae of well-known genera. . . ." Dautzenberg (1889) has very well illustrated the protoconch of an Azorean specimen of *Pedicularia sicula* (Pl. IV, Fig. 2a) and the larva described as an unknown ovulid by Lebour (1945, pages 474–475, Fig. 21) off Bermuda is probably *Pedicularia sicula* (*s.l.*). Hedley (1903, Fig. 69, page 342) also figured the protoconch of a *Pedicularia* species from off New South Wales. Other larvae from the family Ovulidae which have

been previously described are *Simnia patula* by Lebour (1932), *Simnia spelta* and
(?) *Ovula ovum* by Thiriot-Quiévreux (1967). All these forms, though having
certain similarities, can be distinguished from *Pedicularia sicula*. Likewise, the
protoconchs of Cypraeidae in the Muséum National d'Histoire Naturelle in Paris
figured by Ranson (1967) cannot be confused with *Pedicularia* because of differ-
ences in the shell ornamentation. However, because of the scarcity of suitable mate-

FIGURE 6. Geographical distribution of *Charonia variegata* (Lamarck) larvae: filled black
circles = *Charonia variegata* larvae; small open circles = stations where *Charonia variegata*
larvae did not occur. The stippling shows approximate geographical regions from which
post-larval *Charonia variegata* (*s.s.*) are known (Clench and Turner, 1957) and does not
include distributional data of *Charonia nodifera* (Larmarck). Arrows show direction of
surface currents.

rial with protoconchs, it has not been possible to make extensive comparisons with
other forms of Cypraeidae and Ovulidae in the tropical North Atlantic.

The larvae of *Pedicularia sicula* (*s.l.*) were found in the Gulf Stream, the
North Atlantic Drift, the Mediterranean Sea, and the North and South Equatorial
Currents (Fig. 12).

*Relationship between the North and Equatorial Atlantic circulation and dispersal
of teleplanic gastropod veligers.* Two basic patterns of geographical distribution are

distinguishable among teleplanic gastropod veligers. The first of these is that found in such forms as *Charonia variegata, Tonna galea, Philippia krebsii, Pedicularia sicula* (*s.l.*), and *Cymatium parthenopeum*. Larvae of these species were found in all three trans-Atlantic surface currents, *viz.*, the North Atlantic Drift and the North and South Equatorial Currents. Some species such as *Phalium granulatum,*

FIGURE 7. Geographical distribution of the larvae of *Tonna galea* (Linné) (= 1) and *Tonna maculosa* (Dillwyn) (= 2). Small open circles denote stations where no species of *Tonna* veligers were found. Stippled areas show geographical regions where post-larval *Tonna galea* are found to the edge of the continental shelf (Turner, 1946). *Tonna maculosa* post-larvae are known in the eastern Atlantic only from scattered records, specifically in the Canaries (see: Fischer-Piette and Nicklès [1946, pages 45–48] for relevant literature.) Arrows indicate direction of surface currents.

Thais haemastoma, and *Smaragdia viridis* were missing in the North Equatorial Current but moved in a westerly direction on the South Equatorial Current only.

The second basic distributional pattern is that in which larvae were missing in the North Atlantic Drift. Such a distribution is not represented among the ten species considered here, but examples may be found in the gastropod genera *Bursa* and *Cypraea*. These genera evidently have larvae which are dispersed eastwardly on the Equatorial Undercurrent, which provides them with a means for larval trans-

port from the South American to the West African coast (*vide* Scheltema, 1968).

The first distributional pattern is restricted to forms which have eurythermal larvae; otherwise they would not survive the low temperatures of the North Atlantic Drift in which they regularly occur (see 21° C isotherm, Fig. 4). Veligers along the entire periphery of the North Atlantic gyre theoretically can be carried between any two points along its edge. The only limitation to the distance a

FIGURE 8. Geographical distribution of the veliger larvae of *Phalium granulatum* (Born): filled black circles = larvae of *Phalium granulatum;* small open circles = plankton stations where *Phalium granulatum* was missing from tows. Stippled areas denote geographical regions where *Phalium granulatum* post-larvae have been found. The eastern and western Atlantic forms are designated subspecifically as *Phalium granulatum undulatum* and *Phalium granulatum granulatum,* respectively (Abbott, 1968). Arrows show direction of surface currents.

particular larva may be carried is the length of pelagic life in relation to current velocity.

The second distributional pattern appears to be characteristic of stenothermal tropical forms, excluded from the colder northern route across the Atlantic but effectively carried eastward in the warm Equatorial Undercurrent.

There may of course also be some species in which some factors other than temperature limit the geographical distribution of the larvae.

Duration of pelagic larval life and its relationship to the velocity of trans-Atlantic Ocean currents

Ekman (1953) in his volume *Zoogeography of the Sea* concluded that trans-oceanic drift of larvae is unlikely because "on the whole the planktonic stage is too

FIGURE 9. Geographical distribution of *Thais haemastoma* larvae. *Thais haemastoma* is known as post-larvae in the eastern Atlantic from two subspecies, *Thais haemastoma haemastoma* (= 1) and *Thais haemastoma forbesi* (= 2); and in the western Atlantic (in addition to the subspecies *Thais haemastoma haemastoma*), from two additional "subspecies," *Thais haemastoma floridana* (= 3) and *Thais haemastoma haysae* (= 4). The adult distribution of these various "subspecies" is taken from Clench (1947) and Knudsen (1956): 5 = larvae of *Thais haemastoma*; 6 = larvae belonging to the *Thais haemastoma* complex but whose specific identity is uncertain (see Figure 3, a). Small open circles are stations where *Thais haemastoma* was not found. Arrow show direction of surface currents.

short to account for dispersal over thousands of kilometers," but he added that "our knowledge of the duration of larval stages in most animals is very meagre" (page 21). Thorson (1961) in a stimulating theoretical paper has summarized data on the length of pelagic larval life of 195 species of bottom invertebrates and concluded that in most instances the period of larval development was too short to account for larval transport across major ocean basins. Among the 18 proso-

branch species that were considered, not one had a larva with a development of over 9 weeks. Thorson specifically excluded members of tropical gastropod genera from consideration, because he lacked data for the duration of their pelagic larval life. He acknowledged, however, that "true long-distance larvae . . . seem mainly to be associated with tropical seas and to be rare or lacking in temperate and cold regions" (Thorson, 1961, page 473). Mileikovsky (1966) also believes "that the

FIGURE 10. Geographical distribution of *Philippia krebsii* (Mörch) larvae: filled black circles = *Philippia krebsii* larvae; small open circles = plankton stations where *Philippia krebsii* did not occur. The stippling indicates approximate geographical distribution of post-larvae of *Philippia krebsii* (Robertson, 1964; Robertson *et al.*, 1970), which are found to 200 meters depth. The species is presently known in the eastern Atlantic only from the Canary and Cape Verde Islands. Arrows show direction of surface currents.

larval drift of all benthic invertebrates in warmer waters of currents in the tropical regions is more prolonged and lengthy than in their counterparts in waters of temperate and high latitude currents" (page 400, in translation). Since Thorson in his summary article was considering only cold-temperate and boreal species, this information on the length of larval development should not be extrapolated to make conclusions on the dispersal of tropical gastropods in ocean currents.

Lacking experimental data, an approximate measure of the minimum length of pelagic larval development must be obtained indirectly. There are very few

data on the growth of any gastropod veliger larvae. However, the growth rate of the prosobranch *Nassarius obsoletus* (Say) is well known under a variety of laboratory conditions (Scheltema, 1967). Let us assume as an approximation that the average shell growth of *Nassarius obsoletus* between 20 and 25° is representative of all phytoplanktotrophic gastropod veliger larvae. If we use this rate and apply it to the measurement of *Cymatium parthenopeum* larvae an estimated value for the minimum time of pelagic larval development may be obtained. Thus in the species *Cymatium parthenopeum* the total pelagic shell growth is represented by the difference in size between the small embryonic shell on top of the cancellate whorl (Fig. 1, j) and that of the fully developed, ready-to-settle larva, almost 2 mm long (Fig. 1, f). This method has been applied to the other species considered (Table I, left-hand column). Admittedly the estimates are only rough, and the

TABLE I

Estimated duration of the pelagic stage in ten gastropod species having teleplanic larvae

Species	Estimated avg. days required for growth ("developmental period")*	Days held in culture ("delay period")	Total days pelagic
Cymatium nicobaricum	207	113**	320
Cymatium parthenopeum	155	138	293
Charonia variegata	219	57	276
Tonna galea	148	94	242
Tonna maculosa	198	—	(198)
Phalium granulatum	107	—	(107)
Thais haemastoma	62	28**	90
Philippia krebsii	67	ca. 7**	74
Smaragdia viridis	25	30	55
Pedicularia sicula	42	—	(42)

* Based on average growth rate of *Nassarius obsoletus* in laboratory culture (*vide* Scheltema, 1967, Table I, page 261).
** These species were successfully held to settlement in the laboratory.

accuracy of the method depends partly upon the shell geometry of the species being studied and upon the assumption that early growth is linear. However, in the only case where other data are available, the estimate obtained by this method is in fairly close agreement. Hence, Butler (1954) estimated from field data a minimum pelagic life of about 50 days for *Thais haemastoma*, not far off from my estimate of 62 days.

The length of pelagic larval development determined by the method just outlined will most certainly tend to underestimate. Larvae for which the proper algal food is known usually grow faster under ideal laboratory conditions than in their natural environment. Moreover, it is well known that many gastropod species can delay settlement. For example, certain predaceous nudibranchs will delay metamorphosis in the absence of their normal coelenterate prey (Thompson, 1958, 1962; Hadfield and Karlson, 1969), and Fretter and Graham (1962, page 448) report that metamorphosis of *Odostomia* (Pyramidellidae) is accelerated by the presence of the polychaete worm *Pomatoceros* and delayed by its absence. Other

gastropod larvae have a more general response. Thus the intertidal snail *Nassarius obsoletus,* primarily a deposit-feeder, delays settlement in the absence of an appropriate sediment (Scheltema, 1956, 1961), and Kiseleva (1966, 1967) has shown that the prosobranchs *Rissoa splendida* and *Bittium reticulatum* settle preferentially on the alga *Cystoseira.* In some species settlement may be simply a tactile response to a surface, apparently the case with the architectonicid *Philippia krebsii.*

FIGURE 11. Geographical distribution of the larvae of *Smaragdia viridis* (Linné): filled black circles = larvae of *Smaragdia viridis;* small open circles = plankton stations where *Smaragdia viridis* was not found. Stippled areas show approximate regions where post-larval *Smaragdia viridis* is found; eastern and western Atlantic subspecies are respectively designated *Smaragdia viridis viridis* (Linné) and *Smaragdia viridis viridemaris* (Maury). Distributional data are compiled from the collections of the Museum of Comparative Zoology and the Philadelphia Academy of Natural Sciences. Arrows show direction of surface currents.

The larval development of many phytoplanktotrophic gastropod veligers can be divided for convenience into two periods (Scheltema, 1967). The first of these—one of rapid growth and morphological development—may be termed the "developmental period." Its end is marked by the inflection point on the cumulative growth curve and the completion of external morphological development (Scheltema, 1967, page 260, Fig. 4). Larvae are ready to settle at this time. Estimates of the duration of pelagic larval development based on the differences in size be-

tween the embryonic and fully developed larval shell are roughly equivalent to the length of the developmental period.

The second period, termed the "delay period," is terminated by a settlement response. In species with very specific post-larval requirements, such a response can be very precise. Very little further growth occurs during the delay period. Many veliger larvae captured in the open sea have completed the developmental period and reached the delay period. Indeed, it was the constancy in size that confused Craven (1883) into believing that the veliger larvae of the *Sinusigera*-type (Fig. 3, a–j) were fully developed holoplanktonic species. He writes, "The two principal arguments in favor of this view were the great distances from land at which they were often found and the constant dimensions of each species" (page 141). It is the delay period which gives to many species the greatest flexibility in the length of their pelagic larval life.

TABLE II

Velocity of the eastwardly and westwardly flowing currents of the north and tropical Atlantic Ocean

Region	Estimated current velocity km/hr	Estimated number of days required for trans-Atlantic drift
North Atlantic Drift (Bahamas to Azores)	0.5–1.3	128–300
(Bahamas to N. W. Africa)	0.9	400
North Equatorial Current		
(N. W. Africa to West Indies)	0.9–1.2	128–171
South Equatorial Current		
(Gulf of Guinea to Brazil)	1.0–3.2	60–154
Equatorial Undercurrent		
(Brazil to Gulf of Guinea)	2.0	96

Data from (1) Pilot Charts, U. S. Hydrographic Office; (2) direct measurements: Dickson and Evans, 1956, North Equatorial Current; Stalcup and Metcalf, 1966, Equatorial Undercurrent; and (3) drift bottle data: Guppy, 1917; Bumpus and Lauzier, 1965; and W.H.O.I. files courtesy of Mr. Dean F. Bumpus.

I have attempted to obtain some measure of the potential length of the delay period experimentally by culturing larvae caught at sea in plankton nets. The endurance of some veliger species under laboratory conditions is truly remarkable (Table I, column designated "delay period"). Thus *Cymatium nicobaricum* was held for 113 days and *Cymatium parthenopeum* for 138 days. Not all species were successfully held in culture, and some species were not caught during the time that culture observations were made.

Addition of the estimated time of the developmental period to that of the delay period probably gives a better estimate of the maximum pelagic life of a species of gastropod than the estimated developmental period alone (last column, Table I).

One may compare these data for the duration of pelagic life with the current velocities of the major eastwardly and westwardly flowing currents of the North Atlantic Ocean (Table II). Under favorable hydrographic conditions the duration of pelagic larval life of *Cymatium nicobaricum, Cymatium parthenopeum, Charonia variegata, Tonna galea, Tonna maculosa,* and probably *Phalium granulatum* are all

sufficiently long to account for their trans-Atlantic dispersal over any of the four major routes.

The remaining four species, *Thais haemastoma, Philippia krebsii, Smaragdia viridis,* and *Pedicularia sicula* seem to have but little opportunity for trans-Atlantic transport either by way of the North Atlantic Drift or the North Equatorial Current, and only under the most favorable conditions could cross in the South Equa-
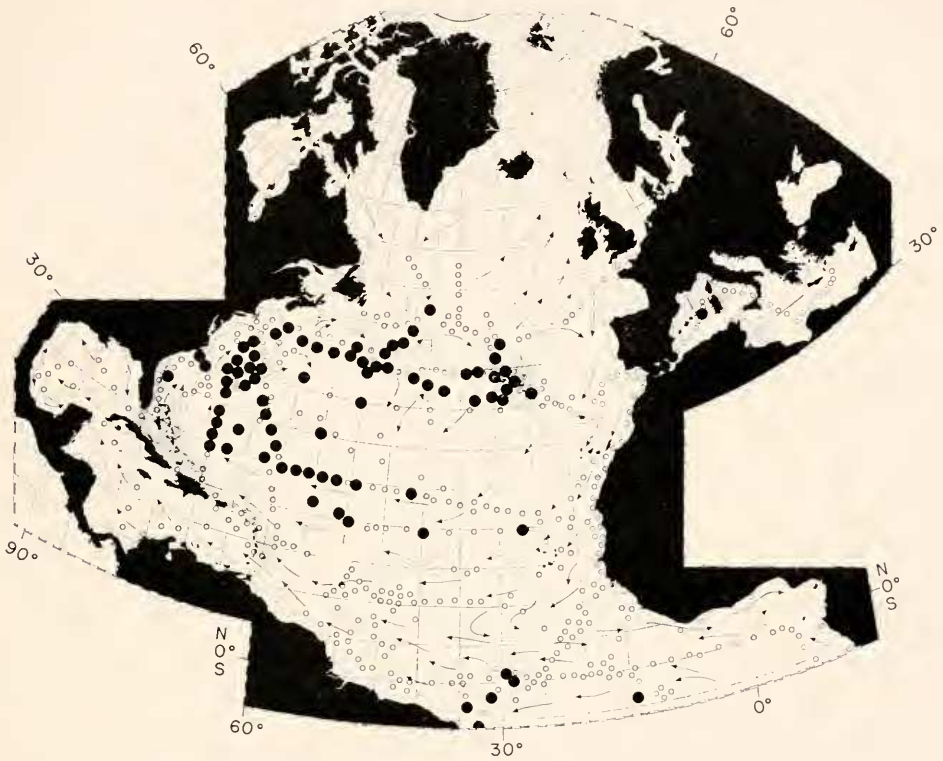

FIGURE 12. Geographical distribution of the larvae of *Pedicularia sicula* Swainson: filled black circles = larvae of *Pedicularia sicula*; small open circles = stations at which larvae of *Pedicularia sicula* were not taken. Stippled areas designate geographical regions from which the post-larvae are known (Allen, 1956). The western Atlantic form *Pedicularia decussata* Gould should probably be regarded as no more than a subspecies of *Pedicularia sicula* (*s.s.*). Arrows show direction of surface currents.

torial Current and the Equatorial Undercurrent. Yet three of the four remaining species under consideration have larvae throughout the entire North Atlantic Drift and two are found also along the North Equatorial Current (see Figs. 9, 10, 11, and 12).

The answer to this paradox must be that the duration of pelagic larval development among these species is longer than estimated. Three possibilities suggest themselves. The first is that the developmental period is much extended under conditions of the open sea. It is known, for example, from observations in the

laboratory that when food is less than optimal, length of the developmental period can be very greatly extended, in some species evidently for months (Millar and Scott, 1967; Turner and Johnson, 1968; personal unpublished observations). It is of course also well known that the amount of phytoplankton in the open sea is very substantially less than in neritic waters. Laboratory experiments show that a reduction in water temperature may extend the length of the developmental period of gastropod veligers up to fifty per cent (Scheltema, 1967, in *Nassarius obsoletus*). This observation is particularly relevant to the duration of pelagic larval development in the North Atlantic Drift as during some months of the year the surface-water temperature there can be ten degrees lower than in the tropical Atlantic.

The second possibility is that the potential length of the delay period may extend over a longer time than has been estimated. Species which as adults have very particular habitats or which prey on specific organisms as food may be suspected of having marked settlement responses. Thus *Pedicularia sicula*, as an adult found only on stylasterine hydrocorals (Robertson, 1970b), may be expected to have a highly developed settlement response. A delay in settlement until a suitable environment is encountered can greatly increase the length of the delay period and the total duration of pelagic existence.

The third possibility is that certain species having relatively small egg capsules may attach these to floating objects, and that the larvae found in the open sea are released subsequently from these capsules. This is clearly not a possibility for the first six species in Table I as their egg masses are quite large and are never attached to floating objects. The capsules of *Thais haemastoma* are relatively small and conceivably could be attached to drifting materials. It is possible that occasionally the adults of certain small species such as *Smaragdia viridis* are mechanically transported, in this instance on turtle grass with which *Smaragdia viridis* is normally associated. Clench (1947, page 76) cites the case of a specimen of *Thais haemastoma* taken from a floating log 300 miles northwest of the Madeira Islands. However, floating objects are seldom seen in the open sea, even in sea-lanes, and in any case could not possibly account for the large numbers of larvae found there.

It is now possible to summarize more specifically the case of the four species in question.

Thais haemastoma is the only species on the list in Table I which shows marked seasonality in its reproduction. Its larva has been found in the North Atlantic Drift only in the autumn, when the falling sea-surface temperature may extend the duration of its larval development (sea-surface temperature is about 21° C during October).

Philippia krebsii is probably able to extend its larval development beyond that suggested by the data in Table I (see also Robertson, 1964, for estimate of length of larval development). In the absence of a tactile stimulus, it can probably greatly extend the duration of its pelagic existence (Robertson *et al.*, 1970).

Probably the larvae of *Smaragdia viridis* are infrequently dispersed across the North Atlantic Drift because of their relatively short planktonic development. The alternative of the adults' drifting on turtle grass is, however, quite possible.

Finally, the delay period of *Pedicularia sicula* larvae, for which there are no data, probably can be extended over long periods. This seems the most reason-

able hypothesis to explain its widespread occurrence in all the North Atlantic surface currents (Fig. 12).

Probability and frequency of long-distance dispersal of veliger larvae

Estimates of the probability and frequency of dispersal from drift-bottle data and survival rates

Larval transport between continents has often been likened to a sweepstakes, because it is believed that the odds that any specific larva will drift across the Atlantic Basin are very small. It is generally concluded from such a quasi-quantitative statement that only rarely can a larva be dispersed in either direction across the Atlantic.

The probability of successful trans-Atlantic larval dispersal, p, depends upon the drift coefficient, p_d, and the survival coefficient, p_s, such that:

$$p = p_d p_s \qquad (1)$$

TABLE III

Percentage drift-bottles released along the North American Coast and subsequently recovered in the Eastern Atlantic Ocean (based on 156,276 bottles) *

Region of recovery	Percentage of total bottles released
Northern Europe (Great Britain, Ireland, Denmark, Norway)	0.10
Azores	0.05
Southern Europe (France, Spain, Portugal)	0.04
Northwest Africa (Including Canary Islands)	0.01
Total percentage recovery in Eastern Atlantic	0.20

* Computed from data in files of Woods Hole Oceanographic Institution and made available through the courtesy of Mr. Dean F. Bumpus.

Specifically, the drift coefficient can be defined as the likelihood that larvae will enter and remain within a current that will transport them across the Atlantic Ocean Basin rather than back onto their own shore. The value of p_d depends upon (1) the distance between the parent population and the ultimate destination of the larvae, that is, the greater the distance the less likelihood for success, and (2) the size of the target area, or, the amount of coastline which the larvae are likely to encounter. An approximate value for the drift coefficient may be derived from a knowledge of drift-bottle and drift-card recoveries. It is assumed that if a larva remains within the surface currents, it will be carried in the same manner as the drift bottles or cards and that consequently the likelihood of its transport across the Atlantic Ocean, other factors being equal, will be similar to that of such bottles or cards. The per cent recovery in both directions, west to east along the North Atlantic Drift and east to west along the North Equatorial Current, is remarkably similar (Tables III and IV), even though the data are from entirely different sources and the sample sizes differ by two orders of magnitude. From

these recovery data an average value of 1.9×10^{-3} may be assigned to p_d. As probably not all bottles that actually make the crossing are eventually recovered, the value of p_d is doubtlessly conservative.

The survival coefficient p_s is the probability that a pelagic phytoplanktotropic larva will survive to settlement without regard to where it may be dispersed. It must include possibility of mortality by predation, disease, or starvation. Because such information is not known for any tropical gastropod veliger, the value for larval survival, p_s, must be derived by an indirect method.

Over the long course of time it is evident that each member of a species must reproduce itself at least once during its lifetime; otherwise the species will decrease in numbers to eventual extinction. Therefore the minimum survival of any viable species must on the average be such that for each member there is produced during

TABLE IV

Percentage drift-cards released along the North-West African Coast and subsequently recovered in the Western Atlantic Ocean (based on 1,800 cards)*

Region of recovery	Percentage of total
Anguilla (British West Indies)	0.06
East Coast of Florida (Cocoa Beach)	0.06
Outer Banks (North Carolina)	0.06
Total percentage recovery in Western Atlantic	0.18

* Data computed from Stander, Shannon and Campbell, 1969, Fig. 1, page 296; Table I, page 294–295.

its lifetime one larva that ultimately survives to sexual maturity. Thus in a dioecious species:

$$p_s = \frac{2}{t_f} \qquad (2)$$

where t_f is the fecundity or total number of eggs produced per female.

The numerator "2" in the expression on the right-hand side of the equation assumes an equal number of males and females in the population. The equation further assumes that chances for survival are equally good in coastal and off-shore waters. The expression probably tends somewhat to underestimate larval survival because it includes post-larval mortality. However, the latter is regarded as being very small compared to the mortality of larvae.

Selected examples can now be considered. Members of the genus *Tonna* are known to produce broad, flat, ribbon-like egg masses with *ca.* 300,000 to 600,000 eggs. Thorson (1940, page 192) estimated that *Tonna* (?) *maculosa* in the Iranian Gulf produced 350,000 eggs and Knudsen (1950, page 98) describes an egg mass of a *Tonna* from off West Africa with 660,000 eggs. It is not known how many egg masses a female produces, but for ease in calculation let us assume that each spawns five per year over a two-year period and every mass contains

500,000 eggs. The probability that a particular larva from an egg mass will survive and ultimately reach the opposite coast of the Atlantic Basin will then be:

$$p = p_d \cdot \frac{2}{t_f} = [1.9 \times 10^{-3}][4 \times 10^{-7}] = 7.6 \times 10^{-10} \tag{3}$$

or approximately one in eighty billion. Butler (1954) reports that each female *Thais haemastoma* produces 500,000 eggs per season, and a result similar to that of *Tonna* will then be obtained. Thus the probability that any specific larva will be transported across the Atlantic Basin is very small. However, what concerns us here is not, as in a sweepstakes, the likelihood that a particular horse will finish, but rather the total number that will complete the race.

It does not only matter what the odds for dispersal of a particular larva may be; what is also important is the total number of larvae that are dispersed (*vide* Simpson, 1952, pages 167–168). If enough larvae are produced, the chances may become very good that at least some veligers will successfully drift across the Atlantic.

Therefore the frequency of trans-Atlantic dispersal is dependent, not only on the probability of such an event, but also on the number of larvae produced by the parent population. Thus,

$$d = pt \tag{4}$$

where d is the frequency of dispersal, and t is the number of larvae produced by a population. The value of t is a function of the population size, t_p, and the number of eggs produced per female, t_f. In a dioecious species, assuming that half of the population is female, the total number of larvae produced is $t_p/2 \cdot t_f$. Assuming once more that the survival coefficient is $2/t_f$ and substituting in (4) above,

$$d = \left[p_d \cdot \frac{2}{t_f} \right] \cdot \left[\frac{t_p}{2} \cdot t_f \right] = p_d t_p \tag{5}$$

which is simply to write that the frequency of dispersal depends upon (1) the probability that larvae will be carried across the Atlantic by the major ocean currents and (2) the size of the parent population from which the larvae originate. Since p_d, the drift coefficient can be assumed to be essentially constant, the frequency of long distance dispersal on the average may be considered as proportional to the size of the population from which the larvae originate (Fig. 10).

But is is characteristic of benthic marine species that have pelagic larvae, that their adult populations on the bottom vary greatly from one year to the next (Thorson, 1946, page 436, Fig. 199; Coe, 1956). Such large changes in population size most frequently reflect the success or failure of planktonic larval development. If large variations in larval survival occur from one year to the next, it follows that the frequency of long-distance dispersal must also fluctuate widely. There are, however, surprisingly few continuous records over long periods which measure such fluctuations. Among the best of such published data are those collected by Loosanoff (1966, 1964) on the settlement of the American oyster *Crassostrea virginica* and its principal predator, the seastar *Asterias forbesi*, in Long Island Sound over a period of 25 years. Between 1937 and 1961, Loosanoff found extremes in

the intensity of settlement from 3 to 42,623 organisms per hundred shell faces
($\cong 0.25$ M^2). The median intensity of settlement was between one thousand and
ten thousand larvae per unit area; during sixteen of the twenty-five years the settle-
ment intensity fell within this range (Fig. 14).

In *Asterias forbesi* the intensity of settlement was more variable from year to
year. Thus, during six of the twenty-five years of observation, the density of settle-
ment per hundred shell faces was between 1 and 10 organisms; during six other
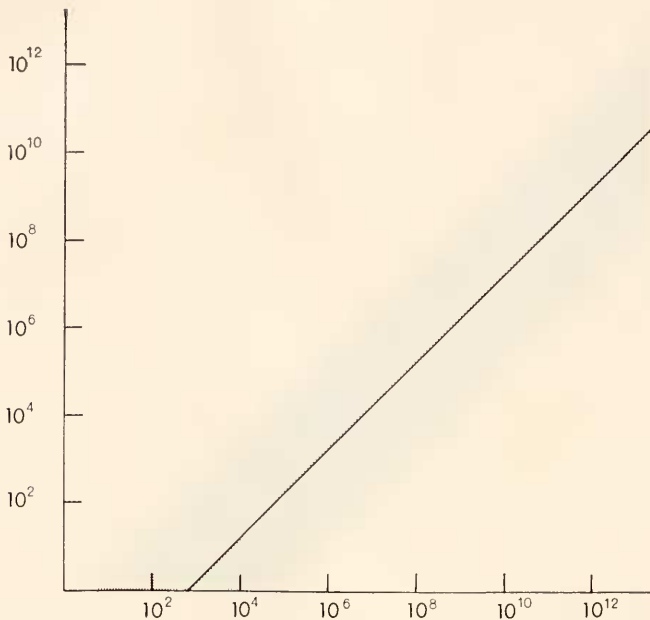
FIGURE 13. Relationship between frequency of larval dispersal (d) and population size
(t_p). The horizontal axis shows population size, and the vertical axis frequency of dispersal.
In this example a value of 1.9×10^{-3} is assumed for the drift coefficient (p_a). This value is
approximate for p_a in the North and Equatorial Atlantic Ocean. The curve shows the ex-
pected frequency of larval dispersal (d) computed from various assumed population sizes
when only one larva survives for each adult member of the parent population. Fluctuations
in larval survival for most benthic species are expected to lie within the stippled region
(*vide* Fig. 11; Thorson, 1946, page 439, Fig. 199; Coe, 1956; Loosanoff, 1964, 1966).

years it fell between 10 and 100 organisms; for nine years it was between 100 and
1000 organisms, and finally during two years it fell between 1000 and 10,000
organisms (Fig. 14). From these and other available data (Thorson, 1946; Coe,
1956) it appears that in most instances the fluctuation in successful settlement will
lie within four and certainly five orders of magnitude. These data allow one to
predict that the variation in the frequency of long-distance dispersal will probably
also fall within similar limits (Fig. 13).

In considering the frequency of long-distance dispersal it has been necessary
to assume that the duration of larval development is sufficient to allow transoceanic

dispersal, because it is not possible to arrive at a coefficient which uniquely represents the length of larval life and yet is biologically unrelated to some character defined by the survival coefficient, p_s.

The theoretical model shows that, over long periods of time (decades or more), the frequency of dispersal is largely dependent upon the parent population size, but that over shorter periods it may be more closely related to survival of the larvae.

Estimates of dispersal frequency from occurrence of larvae in the plankton

A further consideration of evidence from the plankton tows and its relationship to the preceding theoretical model can now be made. It is first necessary to determine the limitations of the collection method. If a plankton net of three-quarter-meter diameter is towed at approximately 5.5 km/hr (3 knots) for twenty minutes and the efficiency of the net is assumed to be ninety per cent, then the

TABLE V

Number of gastropod veligers present in each of the major east-west currents of the North Atlantic Ocean when homogeneous distribution and minimal detectable concentrations of larvae by the present method of sampling are assumed
(Minimum detectable concentration = 1.35×10^{-3} larvae/m^3)

	Volume of water* (m^3)	Total number larvae at conc. of one/tow
North Atlantic Drift	2.45×10^5	3.31×10^{11}
North Equatorial Current	3.43×10^5	4.63×10^{11}
South Equatorial Current	2.26×10^5	3.05×10^{11}
Equatorial Undercurrent	0.98×10^5	1.32×10^{11}

* In computing the sea-surface area of each major ocean current the following co-ordinates when connected by straight lines were arbitrarily considered to enclose the currents: North Atlantic Drift—45°N–60°W; 45°N–20°W; 35°N–10°W; 35°N–72°W; North Equatorial Current—25°N–65°W; 25°N–20°W; 10°N–25°W; 10°N–55°W; South Equatorial Current—5°N–50°W; 5°N–20°W; 5°S–7°E; 5°S–35°W; Equatorial Undercurrent—2°N–35°W; 2°N–5°E; 2°S–5°E; 2°S–35°W.

capture of a single organism represents 1.35×10^{-3} organisms per cubic meter. This figure represents the lower limits of sensitivity obtained by the method of capture. When larvae occur at even lower concentrations, they will not be captured in every plankton tow taken. When their concentration is greater than $1.35 \times 10^{-3}/m^3$ they will be expected to occur more than once in each sample. The numbers of larvae actually taken varied with the species and the distance from the point of their origin. In my samples the numbers ranged from one to over 500 per tow; however, it seldom occurred that more than ten gastropod veliger larvae of any particular species were taken in a mid-ocean sample. Thus the concentration of larvae in most tows, by comparison with the more common holoplanktonic species, was very low.

Even though the concentration of larvae per cubic meter may be small, the volume of water in which the veligers are found is very large. If one arbitrarily delimits the surface area of each of the major east-west currents of the North and Equatorial Atlantic and considers only the upper 50 m (or in the case of the

Equatorial Undercurrent a vertical distance between 50 and 100 m depth) one can compute the volume of water in which most of the larvae are to be found (Table V). Assuming the lowest measurable concentration of one larva per tow, and considering the case in which a single veliger occurs in each sample of a trans-oceanic section, one can now roughly calculate the number of larvae that ought to
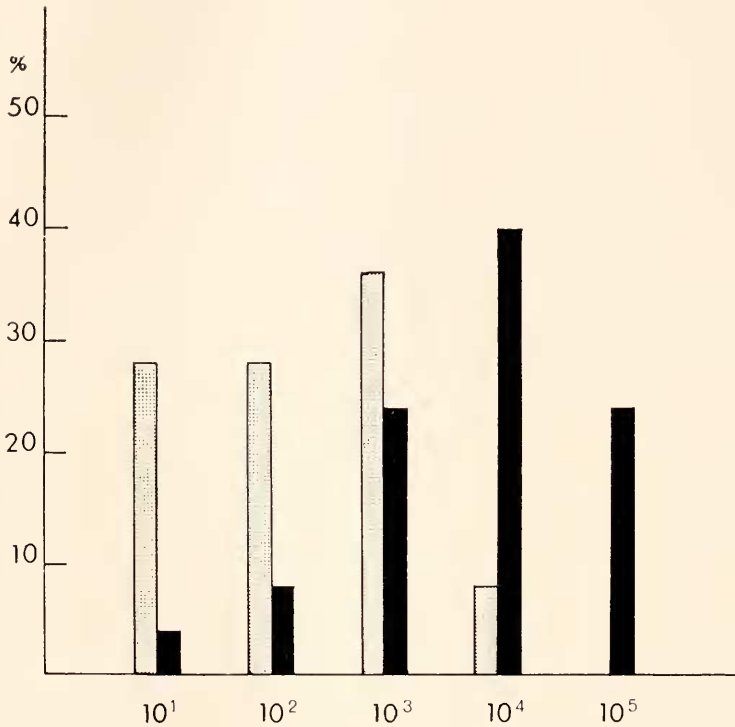

FIGURE 14. Intensity of larval settlement of the sea-star *Asteria forbesi* (stippled bars) and the oyster *Crassostrea virginica* (solid bars) over a period of twenty-five years. The ordinate gives the percentage of years during which settlement occurred at a density value (number/0.25 m²) shown on the abscissa. The success of settlement is regarded as being directly related to larval survival and, at least in the species represented here, the median density of settlement is *approximately* equal to the survival when $p_s = 2/t_f$ (*i.e.*, when each individual in the population gives rise to one offspring). There are other species where the latter relationship is probably not true, specifically, when the frequency-density curve is skewed (data taken from Loosanoff, 1964, 1966).

be present throughout the length of any such current at one instant in time. Thus if the concentration of gastropod veligers is $1.35 \times 10^{-3}/m^3$, the number of larvae in the North Equatorial Current will be

$$[3.43 \times 10^5 \ km^3] \cdot [1.35 \times 10^6 \ larvae/km^3] = 4.63 \times 10^{11}$$

or about 460 billion veligers. East-west sections made across the Atlantic in the North Equatorial Current during the months of January and June show that, in

half of the species considered, larvae occurred during both the winter and summer months. The implication is that the total larvae present in the current may approximately assume a steady state and that as larvae are removed from the western extremity of the current, new ones are added at the eastern end. Assuming a travel time for the larvae of about 170 days (Table II), the number of larvae transported across the Atlantic Basin on the North Equatorial Current each year will be somewhat over two times the total number of larvae present at any one instant.

Perhaps these computations are somewhat fanciful. Actually the larvae are not known to be uniformly distributed, although uniform distribution is of course the underlying assumption in the foregoing calculations. Indeed, none of the species are found in every sample, whereas, on the other hand, many frequently occurred in numbers greater than one per tow. What the computations do clearly indicate is that large numbers of larvae may be dispersed and yet be completely undetected

TABLE VI

Relative frequency at which ten species of gastropod veliger larvae occur in plankton samples from the warm-temperate and tropical surface waters of North Atlantic Ocean (based on 658 samples)

Species	Number of stations found	Percentage of stations found
Cymatium parthenopeum	177	26.9
Philippia krebsii	136	20.7
Pedicularia sicula	114	17.3
Smaragdia viridis	95	14.4
Charonia variegata	91	13.8
Tonna galea	89	13.5
Phalium granulatum	33	5.0
Thais haemastoma	32	4.9
Cymatium nicobaricum	28	4.3
Tonna maculosa	4	0.6

by the present method of sampling. If the larvae of a species can be found in midocean with consistent regularity, it is likely that it frequently will be dispersed across the Atlantic.

The fate of the larvae after they reach their destination is yet another matter. The number of larvae required to have any genetic impact on the recipient population must depend upon the selective advantage that the characters carried by the larvae from their parent population may have in the new environment.

Relative rates of genetic exchange and the apparent effect on geographically separated populations of marine gastropods

The frequency with which a species of larva is found in a series of tows along a section across the Atlantic Basin can give some indication of the rate of transoceanic exchange relative to other veliger species taken from the same samples. As a first approximation the data from all stations in the North and Equatorial Atlantic can be pooled (Table VI). If the frequency of occurrence is expressed as the per cent of all stations at which a species was found and the ten species con-

sidered are accordingly ranked, then *Cymatium parthenopeum* will be at the top of the list, appearing in 26.9 per cent of the samples, whereas *Tonna maculosa* will be at the bottom, being found in only 0.6 per cent of the samples.

Cymatium parthenopeum is a species that as an adult is commonly found in the shelf fauna throughout the warm and tropical North Atlantic Ocean (Clench and Turner, 1957), whereas *Tonna maculosa* is principally found in the western Atlantic, being known only from a few scattered records in the eastern Atlantic (Fischer-Piette and Nicklès, 1946). One can perhaps conclude that *Tonna maculosa* is occasionally re-introduced into the eastern Atlantic and has never become established, or alternately, that it has been consistently overlooked in eastern Atlantic collections.

Notwithstanding its long pelagic larval development (Table I), *Cymatium nicobaricum* has an adult distribution somewhat similar to that of *Tonna maculosa*. In the eastern Atlantic it has been found only on the Madeira and Canary Islands (Clench and Turner, 1957; Odhner, 1931; Dautzenberg, 1890).

Regarding the remaining gastropod species one can ask whether the relative amount of isolation between their eastern and western Atlantic populations is reflected in the degree of morphological difference between them. The assumption is that the degree of difference is inversely related to the amount of genetic exchange between them and that the rate of gene-flow is related to the frequency with which larvae of a particular species are found relative to other species of veligers in the plankton. Hence, the fewer samples in which a veliger species is found, the greater the probability that populations on either side of the Atlantic will be represented by distinct subspecies.

The case of *Philippia krebsii* is problematic since the species is not easily collected as an adult and was not even known to occur in the eastern Atlantic until quite recently (Robertson, 1964; Robertson *et al.*, 1970).

The genus *Pedicularia* in the North Atlantic is often considered to include two species, one on either side of the Atlantic. These two forms are, however, probably best regarded as a single species, perhaps composed of two geographical subspecies. In any case not enough adult specimens are presently available for determining morphological variability of the eastern and western Atlantic forms.

Smaragdia viridis has two subspecies, *viridis* in the eastern Atlantic and *viridemaris* in the western Atlantic, although the frequency of its occurrence appears high on the list. However, 75 per cent of all specimens found in east-west trans-Atlantic currents occurred at the western end of the North Atlantic Drift (Fig. 11). Moreover, the length of its larval development probably limits the frequency of its dispersal (Table I).

Both *Charonia variegata* and *Tonna galea* are highly variable species. Neither are regarded as having geographic subspecies (Clench and Turner, 1957; Turner, 1946).

The percentage of stations at which *Phalium granulatum* is found is considerably less than the preceding two species. *Phalium granulatum* was recently reviewed by Abbott (1968), who considers it to have three subspecies, namely, *undulatum* in the eastern Atlantic and Mediterranean, *granulatum* in the western Atlantic including the West Indies, Central America, and Northern Brazil, and *centriquadratum* in the eastern Pacific from Southern California to Peru.

Near the bottom of the list and perhaps one of the most interesting examples is *Thais haemastoma*. This highly variable species is usually considered to have four subspecies: *haemastoma* and *forbesi* in the eastern Atlantic and *haemastoma, floridana,* and *haysae* in the western Atlantic (Fig. 9). The dispersal in the easterly direction is in the North Atlantic Drift, where it has been found only in the late summer and early fall. Butler (1954) observed that the species breeds in the Gulf of Mexico during June, July, and August. Hence, it is one of the few examples in which there appears to be some seasonality in the occurrence of larvae. Dispersal in a westerly direction is evidently restricted to the South Equatorial Current. Here the larvae have also been found in winter months.

The data on the frequency of larval occurrence may now be briefly summarized. The veliger larvae of *Cymatium parthenopeum, Charonia variegata,* and *Tonna galea* are common throughout the North Atlantic gyre and no geographic subspecies are recognized among these three forms. *Philippia krebsii* and *Pedicularia sicula* (*s.l.*) are both problematic because their geographic distribution and adult morphology have been insufficiently studied. *Smaragdia viridis* and *Phalium granulatum* have restricted larval dispersal and both have eastern and western Atlantic subspecies. *Thais haemastoma,* whose larvae occur even less widely in the open ocean, is regarded as having four subspecies. Finally, *Cymatium nicobaricum* and *Tonna maculosa* evidently are only very rarely dispersed and are known as adults from only a few records in the eastern Atlantic. Thus even with such a relatively crude measure, there seems to be a relationship between the morphological differences found in widely separated populations and the relative rate of genetic exchange by larval dispersal. Although the relationship is imperfect owing to a lack of knowledge in the variability of adult populations of tropical marine gastropods, a perfect relationship is not expected. If the characters transmitted by larvae are unfavorable in the new environment of the recipient population, selection will tend to eliminate their effect no matter what the rate of larval dispersal may be.

There remain many imponderables. Do the slight shell variations that one sees in geographical subspecies really offer any selective advantage? Possibly not, but in the only two genetic investigations published on marine gastropods where this problem has been studied, on *Purpura lapillus* by Staiger (1957) and the detailed study of Struhsaker (1968) on the tropical intertidal species *Littorina picta,* it is shown that differences in the thickness and sculpturing of the shell were related genetically to highly adaptive physiological characteristics. Thus Struhsaker showed that the sculpturing of *Littorina picta* was genetically related to growth rate and survival of the larvae and also to the resistance to dessication by the adult form.

On January 21, 1971, Professor dr. phil. Gunnar Thorson passed on at the
age of 64. He had yet much to offer and his untimely death was a great shock
and a sincere loss. Gunnar Thorson's writings and great enthusiasm have been
a constant source of inspiration since first I read his work in my student days.
When last I saw him in Venice in October 1970, I gave him a manuscript copy of
this paper not knowing that it was to be one of our last intellectual exchanges.
It seems fitting therefore that I should dedicate this paper to the memory of
Prof. Gunnar Thorson.

Summary

1. Ten species of prosobranch gastropod veligers collected from the open wa-
ters of the North Atlantic Ocean have been identified by comparison of their
larval shells with the protoconchs of identifiable juvenile or adult museum speci-
mens. The larvae described are those of *Cymatium parthenopeum* (von Salis),
Cymatium nicobaricum (Röding), and *Charonia variegata* (Lamarck) belonging
to the family Cymatiidae; *Tonna galea* (Linné) and *Tonna maculosa* (Dillwyn)
belonging to the family Tonnidae; *Phalium granulatum* (Born) belonging to the
family Cassidae; *Thais haemastoma* (Linné), a muricid; *Philippia krebsii*
(Mörch), an architectonicidae; *Smaragdia viridis* (Linné), a neritid; and *Pedi-
cularia sicula* Swainson belonging to the family Ovulidae.

2. The geographical distribution of the veligers of these ten gastropod species
has been determined in the North and tropical Atlantic from approximately eight
hundred and fifty plankton tows. The relationship between the North and Equa-
torial Atlantic circulation and the dispersal of gastropod veliger larvae can be seen
from these data (Figs. 5–12). *Charonia variegata, Philippia krebsii,* and *Pedi-
cularia sicula* were found in all three trans-Atlantic currents sampled, namely,
the eastwardly moving North Atlantic Drift and the westwardly flowing North
and South Equatorial Current. *Cymatium parthenopeum* and *Tonna galea* were
found throughout the North Atlantic gyre, but only from scattered records in
the South Equatorial Current. *Phalium granulatum* and *Thais haemastoma* were
found in the North Atlantic Drift and South Equatorial Current. These seven
species are regularly dispersed in either direction across the North Atlantic bar-
rier. *Smaragdia viridis* was found in the western half of the North Atlantic
Drift and in the eastern half of the South Equatorial Current; it is probably less
frequently transported across the Atlantic. *Cymatium nicobaricum* veligers were
found only once in mid-ocean in the North Atlantic Drift; all other records were
restricted to the tropical and warm temperate Western Atlantic. *Tonna maculosa*
veligers were found only in the Gulf Stream. The adults of all ten species are
amphi-Atlantic in their geographical distribution and occur in the tropical and

warm-temperate shelf waters. Adults of *Cymatium nicobaricum* and *Tonna maculosa,* however, are known from only a few records in the eastern tropical Atlantic.

3. The duration of pelagic larval development has been estimated for the same ten species of gastropods. Six species, *Charonia variegata, Cymatium parthenopeum, Cymatium nicobaricum, Tonna galea, Tonna maculosa,* and *Phalium granulatum* have a period of pelagic development of over three months. *Pedicularia sicula* and *Smaragdia viridis* can probably reach the settling state in less than two months. It is possible that the latter four forms have settling responses and can delay metamorphosis. A comparison between the duration of larval development and the velocity of the North and tropical Atlantic surface currents shows that transoceanic dispersal of the first six mentioned species is possible even without a delay in settlement.

4. The frequency of long-distance dispersal across ocean basins is chiefly dependent upon (a) the drift coefficient, that is, the probability that larvae will be carried off-shore into the major ocean surface currents rather than retained in the coastal waters of the parent population, and (b) the size of the parent population from which the larvae originate. There may be considerable variation in the frequency of long-distance dispersal related to larval mortality.

5. The lower limits of sensitivity obtained by using a conventional plankton net are such that it is possible for trans-oceanic dispersal to occur and yet go completely unnoticed. The concentration of only one larva per tow reoccurring at each station along a transect across the Atlantic may represent a significant amount of trans-oceanic dispersal.

6. If pelagic larvae are important in maintaining genetic continuity, then the degree of morphological differentiation between eastern and western Atlantic populations of gastropod species having amphi-Atlantic distributions would be expected to bear an inverse relationship to the frequency with which the veliger larvae of these species were found in the plankton of the open sea. The evidence from the gastropod species considered here seems to support this hypothesis (Table V).

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